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Early Environmental Conditions Shape Personality Types in a Jumping Spider

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Individuals of many species across the animal kingdom are found to be less plastic than expected, even in behavioral traits. The existence of consistent behavioral differences between individuals, termed "personality differences", is puzzling, since plastic behavior is considered ideal to enable animals to adaptively respond to changes in environmental conditions. In order to elucidate which mechanisms are important for the evolution of personality differences, it is crucial to understand which aspects of the environment are important for the development of personality differences. Here, we tested whether physical or social aspects of the environment during development influence individual differentiation (mean level of behavior) using the jumping spider *Marpissa muscosa*. Furthermore, we assessed whether those behaviors were repeatable, i.e. whether personalities existed. We applied a split-brood design and raised spider siblings in three different environments: a deprived environment with no enrichment, a socially and a physically enriched environment. We focused on exploratory behavior and repeatedly assessed individual behavior in a novel environment and a novel object test. Results show that the environment during development influenced spiders' exploratory tendencies: spiders raised in enriched environments tended to be more exploratory. Most investigated behaviors were repeatable (i.e., personalities existed) across all individuals tested, whereas only few behaviors were also repeatable across individuals that had experienced the same environmental condition. Taken together, our results indicate that external stimuli can influence the development of one aspect of personality, the inter-individual variation (mean level of behavior), in a jumping spider. We also found family by environment interactions on behavioral traits potentially suggesting genetic variation in developmental plasticity.

Keywords: animal personality, arachnids, arthropod, behavioral syndromes, exploration, rearing, salticid, temperament

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INTRODUCTION

Consistent behavioral differences among individuals of the same population are widespread across various taxa in the animal kingdom (reviewed in e.g., Gosling, 2001; Bell et al., 2009; Kralj-Fišer and Schuett, 2014). This means individuals differ in their mean level of behavior (inter-individual behavioral variation) while being (more or less) consistent in their behavior over time and/or different contexts (intra-individual consistency). The existence of such personality differences is puzzling, given that it would seem sensible for individuals to be plastic and to adjust their behavior adaptively to changes in the environmental conditions (e.g., Sih et al., 2004).

Hypotheses that explain the adaptive value of animal personalities are linked to information use (McElreath and Strimling, 2006; Wolf et al., 2008), life-history (McElreath et al., 2007; Wolf et al., 2007), sexual selection (Schuett et al., 2010), and social interactions (McNamara et al., 2009) amongst others (Mangel, 1991; Dall et al., 2004; Nettle, 2006; Réale et al., 2007; Dingemanse and Wolf, 2010), yet empirical tests of these hypotheses remain scarce (but see e.g., Schuett et al., 2011b; Kralj-Fišer and Schneider, 2012; Nicolaus et al., 2012; Schuett et al., 2015). In order to understand the evolution of personality differences, it is also crucial to elucidate the development of personality differences. There is a general consensus that across species, on average about 30% of inter-individual variation in behavior (e.g., Stirling et al., 2002; van Oers et al., 2005; Quinn et al., 2009; van Oers and Sinn, 2011) and about 50% of personality variation is genetically inherited (Dochtermann et al., 2015), while the remaining variation originates from environmental sources (Buss and Greiling, 1999). In particular, environmental conditions experienced during early life may contribute to the development of personality differences by directing individuals into different life-history strategies and personalities ("early experiential calibration", Buss and Greiling, 1999; see also Carere et al., 2005). It has been proposed that similar to life-history traits, personality traits can adjust within a genetically predetermined reaction norm (see e.g., Dingemanse et al., 2010; Groothuis and Trillmich, 2011). As for developmental behavioral plasticity in general, the potential for these plastic responses might be restricted to sensitive periods during ontogenesis (e.g., Groothuis and Trillmich, 2011; or "developmental windows": Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011), since changing an once adopted behavioral phenotype is associated with cost (reviewed in Snell-Rood, 2013). These processes can therefore lead to consistently different phenotypes even with similar genotypes (see Sih et al., 2004; Luttbeg and Sih, 2010) and these differences may be under frequency dependent selection (Lichtenstein and Pruitt, 2015).

To truly understand the evolution of personality differences, we need a comprehensive understanding of the specific environmental aspects shaping the development of personality differences (see Duckworth, 2010; Stamps and Groothuis, 2010). Previous studies have already shown developmental effects on mean behavioral levels such as social interactions (Iba et al., 1995; Arnold and Taborsky, 2010; Ballen et al., 2014; Liebgold, 2014), motor activity (Carducci and Jakob, 2000; Buchsbaum and Morse, 2012), or parental care (Margulis et al., 2005; Branchi et al., 2006). More studies are now desirable that investigate whether behavioral differences induced by developmental effects are consistent and stable, i.e., whether environmental conditions experienced influence animal personalities. Indeed, there is an increasing number of studies focusing on the development of animal personality (e.g., Sinn et al., 2008; Brodin, 2009; Schuett et al., 2011a; Gyuris et al., 2012; Hedrick and Kortet, 2012; Niemelä et al., 2012b; Petelle et al., 2013; Sweeney et al., 2013; Tremmel and Müller, 2013; Guenther et al., 2014; Johnson et al., 2015). To clearly identify underlying processes, experimental studies in which environmental conditions are manipulated are needed. The majority of studies that measured personality development in an experimental setting manipulated either food availability (e.g., Carere et al., 2005; Edenbrow and Croft, 2013), or stress by inducing immune challenge (e.g., Butler et al., 2012; DiRienzo et al., 2015), by increasing antipredator pressure (e.g., Bell and Sih, 2007; Niemelä et al., 2012a; Edenbrow and Croft, 2013), or by preventing access to shelter (Bengston et al., 2014).

Another aspect (potentially overlapping with above mentioned environmental aspects), which might influence the development of personality, is the complexity of the environment itself. Studies on animal intelligence have shown that increasing complexity in the social and/or in the physical environment induces behavioral and neural responses across different taxa (see e.g., Renner and Rosenzweig, 1987; Schrijver et al., 2004; Gonda et al., 2009; Brockmark et al., 2010; Kotrschal et al., 2012). This suggests that an increase in complexity directs animals to develop enhanced cognitive abilities allowing them to cope with increased information. Increased cognitive abilities (i.e., the ability to perceive and compute information) may itself lead to changes in individual behavior and life-history strategies (reviewed e.g., in Mettke-Hofmann, 2014; Trompf and Brown, 2014). Therefore, we assume that exploratory behavior, for example, should be generally positively linked to the amount of information (i.e., the complexity) available in the environment because knowledge of the environment allows behaving adaptively (at least up to a certain point; compare e.g., Niemelä et al., 2013). If, however, information gathering is potentially harmful individuals may show less exploratory tendencies. Such potentially harmful situations might be predation risk or risky interactions with conspecifics. To date, only few studies have investigated the effect of environmental complexity on personality either by increasing the social (Carere et al., 2005; DiRienzo et al., 2012) or the physical complexity (Bolhuis et al., 2005; Fox and Millam, 2007). Also, it remains unclear whether both aspects induce similar or different responses as these two aspects have rarely been manipulated in conjunction (but compare Carere et al., 2005; Bengston et al., 2014). A better understanding of these aspects is essential for elucidating which mechanisms are important for generating and maintaining personality.

In this study we investigated the effects of the social and the environmental complexity as well as genetic effects on the development of personality types using the jumping spider *Marpissa muscosa*. Jumping spiders are active hunters, have highly developed eyes and are sensitive to multiple aspects of their environment (Foelix, 2011). Therefore, we expect their personality development to be influenced by external stimuli (see for an example Royauté et al., 2014), including environmental complexity. Furthermore, we expect exploratory behavior to be a highly relevant behavior for jumping spiders because, among others, they need to search for prey, shelter, and mates. Carducci and Jakob (2000) showed indeed that jumping spiders reared in a physically enriched environment were on average more exploratory later in life. Here, we also added a social component to compare potential effects of the physical environment with effects of the social enrichment (see above).

We used a split-brood design and raised jumping spider siblings in three different environments: a deprived environment

with no enrichment, a socially, and a physically enriched environment. This design allowed us to test for family effects, environmental effects, and their interaction on personality (mean level of behavior; behavioral repeatability within and among treatment groups) and plasticity. We repeatedly measured individual behavior in a novel environment and towards a novel object, and interpreted these as measures of exploratory behavior (see e.g., Réale et al., 2007). We predicted that enrichment, both physical and social, would lead to the development of more exploratory personalities (mean level of exploratory behavior) because information gathering in complex environments should be more advantageous than in less complex or deprived environments. However, we predicted that on average group living spiders might be less exploratory than physically enriched spiders due to the risk of harmful interactions with conspecifics. Even though *M. muscosa* are not considered social animals, they repeatedly interact with conspecifics in their natural environment (on and beneath the bark of trees). Furthermore, we assessed whether, beside those predicted effects on the mean behavioral level, behavior was also repeatable among and within treatment groups, i.e., whether personalities existed in the investigated traits. Finally, by presenting two different analytical approaches (i.e., analyzing repeatability over the whole data set vs. within each treatment separately) we want to highlight the possibility of obtaining different results when ignoring potential effects of developmental background on behavior. For example, the characteristics of the study area (from which individuals are sampled), such as the area's size, might influence the likelihood to detect personality differences: with increasing area the environmental heterogeneity often increases, too, and with it maybe also the potential of detecting (environmentally-induced) personality differences.

METHODS

Rearing Conditions

A total of 160 individuals of 14 maternal lines participated in the experiment. These were derived from three different cohorts and were assigned to one of three experimental groups (for details see below and **Table 1**).

In June–July 2012 we collected in total 18 adult and 17 subadult females and 18 males in northern Germany. Those females, which did not produce eggsacs in captivity (i.e., had probably not yet successfully mated in the field), were mated in the laboratory (by placing the female with a male in a box over night; males were used only once). Females were held solitary in plastic boxes (145 × 110 × 68 mm) enriched with some dry leaves, bark and white tissue paper. For the experiments we used spiderlings derived from the nine females, which were first to produce offspring. Eggsacs were separated from these females 2 weeks after they had been built to prevent any post-hatching maternal effects. After hatching juvenile siblings were assigned to one of three treatments pseudo-randomly (to ensure a balanced number of siblings in all treatments): a "deprived", a "physically enriched", or a "socially enriched" treatment.

TABLE 1 | Summary of sample sizes.

Treatment	Cohort 1	Cohort 2	Cohort 3	∑
d	11	18	22	51
p	20	16	22	58
g	13	10	28	51
∑	44	44	72	–

Numbers of individuals are given for each treatment group (d = "socially and physically deprived"; g = "socially enriched"; p = "physically enriched") and for each cohort. For more details please see text.

In all three treatments, spiders were held in translucent plastic boxes with holes that were covered with blue gauze to ensure air circulation. We raised spiders in the "deprived" treatment (treatment: "d") alone and without visual contact to conspecifics in boxes of 98 × 58 × 35 mm size. The bottom of the box was covered with white tissue paper and a small ball of the same material was included to give the spiders the opportunity to hide. Spiders in the "physically enriched" treatment (treatment: "p") were raised alone and without visual contact to conspecifics in boxes of 145 × 110 × 68 mm size. These boxes were enriched with both natural and artificial objects [such as bark, Iceland moss (*Cetraria islandica*), dry leaves, orange colored cords, Lego©bricks, bottle caps]. We increased the degree of enrichment over the weeks until an age of 46 weeks (by which time most spiders had reached maturity) and we altered the arrangement of objects every other week. Also a wooden plateau was included to increase the surface and structure of the box. The bottom of the box was covered with white tissue paper. In the "socially enriched", group treatment (treatment: "g") siblings were held together in groups of five to 15 individuals in one box (mean ± SE = 8.1 ± 3.3). The actual number of individuals per group depended on the total clutch size from which the siblings were allocated to the treatments, i.e., only siblings from large clutches reached the maximum size of 15 group members. The size of the box was matched to the actual group size so that on average each spider had a surface area of roughly 222 cm^2, which is similar to the area in the deprived treatment. The bottom of the box was covered with white tissue paper and a few paper balls were included to provide cover. In the socially enriched treatment, we separated spiders from their group when they reached subadulthood (at mean ± SE = 44 ± 8.4 weeks) to prevent uncontrolled matings. The new boxes had the same size and content as in treatment "d" but were put in close proximity to facilitate visual contact among conspecifics.

All animals were kept in the same laboratory room under constant conditions with a 17:7 h light:dark regime and temperatures between 22 and 24°C. Humidity was between 30 and 60% in the room (higher in boxes due to regular spraying into boxes). Depending on its age we fed each spider with 3–15 *Drosophila* spec. per week. Because spiders were held in groups in the social treatment the number of flies consumed by individual spiders might have varied. A total of five cannibalistic acts were observed in four out of twelve social groups. Every other week we monitored the developmental stage of each spider (juvenile, subadult, or mature) by inspecting the reproductive organs. At maturity the pedipalps of males are differentiated and turn dark

and the epigyne of females becomes more pronounced and turns dark.

In 2012, we lost 56 of 142 spiderlings through unsuccessful molting or escapes (equally distributed across treatments: unsuccessful molting: GLM, $\chi^2 = 0.745$; $p = 0.689$; escapes: GLM, $\chi^2 = 4.368$; $p = 0.113$). To compensate for the reduction in sample size we also included individuals from family groups in which spiderlings had been raised together in a physically deprived environment for 2 months after hatching within larger groups (11–35 spiderlings per group). We pseudo-randomly assigned these spiders into the three treatments groups as described above. In the following we will refer to the original spiders as "cohort 1", to the spiders that were included later to compensate for the loss of individuals as "cohort 2".

In June 2013, we collected additional 23 adult, and presumably mated, females from the field. The offspring of five of those females were used to create cohort 3. These spiderlings were raised in similar ways to cohort 1 with some minor variations: we constantly provided small plastic tubes filled with wet cotton wool to prevent dehydration problems. Secondly, in the first week hatchlings received a sugar water drop in addition to the three flies. Finally, to prevent hatchlings from escaping their boxes (in the deprived treatment) they were held in plastic cylindrical containers (5.5 cm diameter). After 10 weeks they were transferred to the standard boxes described above for the deprived treatment.

Behavioral Tests

We tested all individuals twice each for their behavior in an open field and towards a novel object. In total, we recorded eight different behaviors during these tests of which seven were analyzed (see below; **Table 2**). Behavioral tests took place in a soundproof room with no windows between 16.07.2013 and 10.08.2013 for cohort 1 and 2 when spiderlings were 51.0 (± 0.85 SD) and 52.2 (± 1.9 SD) weeks of age, respectively. Spiders of cohort 3 were tested between 27.02.2014 and 26.03.2014 aged 35.1 (± 0.97 SD) weeks. All individuals were retested after 7 days to determine behavioral consistency. We tested three individuals simultaneously, if possible one from each (49%) or at least from two (40%) treatments. All spiders were tested in visual isolation from one another.

The open-field test started after a 30 min acclimatization phase to the test room. In a similar approach to Carducci and Jakob (2000) we divided the arena (a plastic box 145 × 110 × 68 mm) into 30 small quadratic fields (2.80 × 2.90 cm) with a central and an edge area to quantify activity (see **Figure 1**). Acclimatization started after the spider was put into a white opaque plastic cap (5.5 cm diameter, 1.2 cm high, **Figure 1**). The cap was half-covered with gray plastic foil to generate cover for the spiders. The rationale was that the cap would function as a safe retreat that the spiders would only leave when motivated to explore the open field. Spiders were given a total of 60 min to climb out of the start cap and to explore the arena. If spiders did not leave the start cap we removed them from analyses for that trial (in the first trial: d: $N = 3$, g: $N = 6$, p: $N = 4$ and in the second trial: d: $N = 3$, g: $N = 2$, p: $N = 2$).

TABLE 2 | Variables recorded from the open field (OF) and novel object (NO) test as measures of exploratory behavior.

Variable name	Description	Test
Latency to emerge OF	Latency to leave the start cap	Open field
Percentage of area visited OF	Percent of fields visited	Open field
Visitation central area OF	Whether (yes/no) the individual entered the central area in the last 7.5 min	Open field
Activity in central area OF	Duration of being active in the central area relative to the total exploration time, i.e., after leaving the start cap	Open field
Resting OF	Total duration of resting once the spider had left the start cap (>3 s without movement)	Open field
Touched NO	Whether (yes/no) the spider touched the NO or not	Novel object
Latency NO	Latency to touch the object (of those who did touch the NO)	Novel object

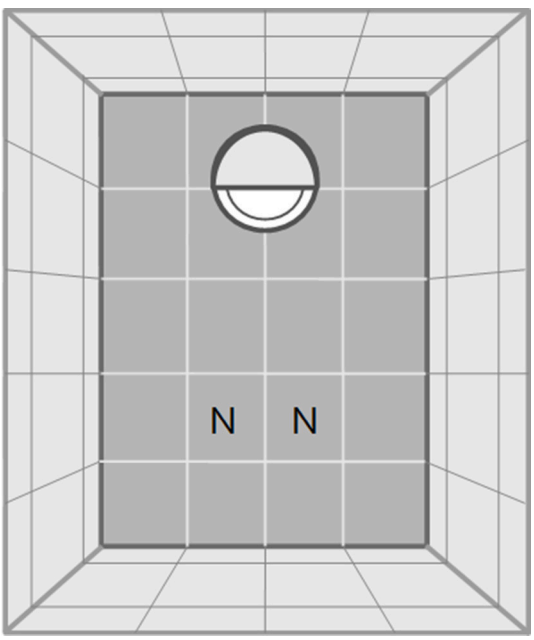

FIGURE 1 | Schematic drawing of the test arena for both, the open field and the novel object test. Dark gray fields indicate ground, light gray fields indicate walls. In one end of the arena a white opaque plastic cap is shown which functioned as start point. The cap was half-covered with gray plastic foil to generate shelter for the spiders. The letters "N" indicate the two possible positions in which the novel object was introduced at the beginning of the novel object test. The drawing is not to scale.

After the open field test we transferred spiders back into the plastic cap, which was covered to prevent spiders from climbing out. A novel object (a greenish wooden barrel: 1.5 cm diameter, 1 cm high) was placed at the opposite end of the arena (**Figure 1**). After removal of the cover of the cap the spiders were allowed to explore the arena and the novel object for 30 min.

We videotaped the behavior and the experimenter (D.R.) left the room for the duration of the tests. After each test the arenas and novel objects were cleaned with water.

Video Analysis

All video clips were anonymized and randomized by a third person before being analyzed (by D.R.). For the open field test we analyzed the first 7.5 min and at minutes 22.5–30 of each trial (15 min total). The remaining minutes were not included in order to reduce time of analyzing. For the novel object test all 30 min were analyzed.

Data Analyses

All analyses were done using R 3.1.0 (R Core Team, 2014) except calculations using the R package "rptR" (Schielzeth and Nakagawa, 2011) for which we used R 2.15.1 (R Core Team, 2012) because this package was not yet implemented for latest R versions.

In order to explore whether different behavioral variables correlated with one another we ran Spearman rank correlations with data obtained from the first trial. To avoid duplication of results we excluded the total number of fields visited during the open field test (visits and revisits) which correlated strongly with the percentage of total area visited in the open field ("percentage of area visited OF"; $r_s = 0.606$; $p < 0.001$). All other variable combinations correlated only moderately or less ($r_s < 0.42$) and thus a total of seven variables were included in further analyses (see **Table 2**). We also ran a principal component analysis to reduce the number of variables. However, sufficient principal components together should account for 90 % of the total variation (Crawley, 2013). In our case this would have meant to use nearly as many components as original variables. We therefore only used the original variables which are easy to interpret and facilitate comparison with other studies.

To assess the influence of our treatments and cohorts on the behavioral level of individuals, we used several GEEs (general estimated equations); GEEs are extensions of GLMs and are a robust way for analyzing correlated data (here: data of individuals from the same family) and especially useful when comparing population averages (Liang and Zeger, 1986; Quinn and Keough, 2002; Zuur et al., 2009; Zhang et al., 2012). We used the R package "geepack" (Halekoh et al., 2006) to estimate the effects of rearing conditions (treatment and cohorts) on the population mean level of the in **Table 2** mentioned seven behavioral variables obtained from the first test series. Thus, each individual contributed only one data point for these analyses. To account for potential family effects, we included the ID of the mother as cluster variable. In all models we included the two-way interactions between treatment and cohort and between treatment and sex as explanatory variables, as well as their main effects. We also included the variables "latency to emerge OF" and "latency to emerge NO", respectively, in the analyses because we wanted to control for differences in the actual duration each individual had spent in the arena outside of the start cap. The "latency to emerge OF" was not included in the analysis of the variable "activity in central area OF" which is a relative estimate. Here, the variation in the time in the arena is already corrected for by different start times. Because many spiders did not touch the novel object (37 of 141) and thus were removed for estimations of the depending variable "latency NO" we excluded the factor "sex" in this analysis as not to overly decrease the sample size (the sex could not be determined for all individuals).

Prior to analysis we excluded missing data so that sample sizes vary for different analyses (see **Table 3**). If required, variables were transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011) or adequate error structures were used to meet model assumptions (i.e., binomial error structure for binary data; see **Table 3**). Maximal models were simplified step-wise by taking each term out in turn, then excluding the least significant term at each step, starting with interactions first, given the removal of a term did not significantly reduce the explanatory power of the model (Crawley, 2002). We tested whether the explanatory power of the simpler model was significantly reduced compared to the more complex model using Wald statistics (Zuur et al., 2009). Model simplification was continued until the minimal model was found, i.e., the model which included only significant explanatory variables (or main effects which were included in significant interactions). *P*-values and associated test statistics given for non-significant terms come from the time a term dropped out of the model (see **Table 3**). When the rearing variables (treatment p, d, and g and cohorts 1, 2, and 3) were not included in significant interactions but had significant effects on the response variable, we checked for differences between the levels by merging factor levels (compare Crawley, 2002) and compared the explanatory power of the simpler and more complex model. *P*-values given come from these comparisons (see **Table 4**). Please note that we did not adjust *p*-values for multiple comparisons.

To assess behavioral consistency we estimated behavioral repeatabilities and their 95% confidence intervals from generalized linear mixed effects models using R package "rptR" (with 1000 bootstraps and permutations; Nakagawa and Schielzeth, 2010). If confidence intervals did not include zero, repeatability was regarded as significant. We analyzed repeatability over the whole data set (**Table 5**) and within each treatment separately (**Table 6**). As above noted we did not adjust *p*-values for multiple comparisons. For further details on the specific models used, please see **Tables 5, 6**.

To test whether the degree of behavioral consistencies differed among treatment groups, we would have needed to test whether repeatability differed significantly among treatments. Yet, sample sizes within each treatment were rather low and many behavioral variables were not repeatable within each treatment group (see **Table 6**). Therefore, we only tested whether the population mean level of behavior differed among treatment groups and whether those behaviors were stable over all individuals (regardless of the environment they had experienced), i.e., whether measured behaviors are personality traits in the species.

In further analyses we investigated genotype by environment interactions. We used the maternal line as a proxy for genotype (but please note that individuals within a family were not genetically identical and that we cannot rule out pre-hatching maternal effects; we therefore use the term "family by environment" interaction). We fitted generalized linear models,

TABLE 3 | Model outputs (GEEs) indicating effects on the mean level behavior shown in an open field test (OF) and a novel object test (NO).

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Latency to emerge OF	Gaussian	136	Mean	4.788	0.187		
			Treatment × Cohort			$\chi^2_{(4)} = 1.52$	$p = 0.82$
			TreatG:Cohort2	(−0.363)	(0.602)		
			TreatP:Cohort2	(0.284)	(0.399)		
			TreatG:Cohort3	(−0.157)	(0.468)		
			TreatP:Cohort3	(−0.256)	(0.567)		
			Treatment × Sex			$\chi^2_{(2)} = 2.04$	$p = 0.36$
			TreatG:SexF	(−0.620)	(0.451)		
			TreatP:SexF	(−0.325)	(0.391)		
			Treatment			$\chi^2_{(2)} = 11.5$	$p =$ **0.003**
			TreatG	−0.268	0.557		
			TreatP	−0.339	0.532		
			Cohort			$\chi^2_{(2)} = 25.0$	$p <$ **0.001**
			Cohort2	0.077	0.207		
			Cohort3	−0.858	0.192		
			SexF	(0.231)	(0.189)	$\chi^2_{(2)} = 1.5$	$p = 0.22$
Percentage of area visited OF	Gaussian	135	Mean	12.391	0.437		
			Treatment × Cohort			$\chi^2_{(4)} = 1.67$	$p = 0.8$
			TreatG:Cohort2	(−0.816)	(2.252)		
			TreatP:Cohort2	(−0.635)	(1.097)		
			TreatG:Cohort3	(−1.406)	(1.594)		
			TreatP:Cohort3	(−1.129)	(1.099)		
			Treatment × Sex			$\chi^2_{(2)} = 1.26$	$p = 0.53$
			TreatG:SexF	(−1.524)	(1.439)		
			TreatP:SexF	(−0.281)	(1.055)		
			Treatment			$\chi^2_{(2)} = 15.7$	$p <$ **0.001**
			TreatG	−0.116	0.616		
			TreatP	1.266	0.400		
			Cohort			$\chi^2_{(2)} = 2.22$	$p = 0.33$
			Cohort2	(0.328)	(0.563)		
			Cohort3	(1.012)	(0.752)		
			SexF	(0.180)	(0.240)	$\chi^2_{(1)} = 0.56$	$p = 0.45$
			Latency to emerge OF	−0.005	0.001	$\chi^2_{(1)} = 40.8$	$p <$ **0.001**
Visitation central area OF	Binomial	135	Mean	0.009	0.796		
			Treatment × Cohort			$\chi^2_{(4)} = 25.6$	$p <$ **0.001**
			TreatG:Cohort2	0.335	0.914		
			TreatP:Cohort2	0.842	1.092		
			TreatG:Cohort3	−1.914	0.347		
			TreatP:Cohort3	1.108	1.159		
			Treatment × Sex			$\chi^2_{(2)} = 2.08$	$p = 0.35$
			TreatG:SexF	1.513	1.066		
			TreatP:SexF	0.293	0.818		
			Treatment				
			TreatG	1.225	0.288		
			TreatP	0.111	0.760		
			Cohort				
			Cohort2	−0.666	1.080		
			Cohort3	−0.460	0.904		
			SexF	−0.643	0.374	$\chi^2_{(1)} = 2.95$	$p = 0.086$
			Latency to emerge OF	0.001	0.001	$\chi^2_{(1)} = 1.0$	$p = 0.32$

(Continued)

TABLE 3 | Continued

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Activity in central area OF	Gaussian	114	Mean	0.508	0.050		
			Treatment × Cohort			$\chi^2_{(4)} = 13.8$	$p = \mathbf{0.008}$
			TreatG:Cohort2	0.045	0.054		
			TreatP:Cohort2	−0.098	0.051		
			TreatG:Cohort3	−0.006	0.045		
			TreatP:Cohort3	−0.095	0.053		
			Treatment x Sex			$\chi^2_{(2)} = 4.22$	$p = 0.12$
			TreatG:SexF	(−0.031)	(0.036)		
			TreatP:SexF	(−0.071)	(0.035)		
			Treatment				
			TreatG	−0.016	0.039		
			TreatP	0.074	0.048		
			Cohort				
			Cohort2	0.015	0.053		
			Cohort3	−0.025	0.059		
			SexF	(−0.008)	(0.015)	$\chi^2_{(1)} = 0.30$	$p = 0.59$
Resting OF	Gaussian	132	Mean	0.787	0.041		
			Tratment × Cohort			$\chi^2_{(4)} = 5.89$	$p = 0.21$
			TreatG:Cohort2	(−0.071)	(0.059)		
			TreatP:Cohort2	(−0.030)	(0.031)		
			TreatG:Cohort3	(−0.088)	(0.039)		
			TreatP:Cohort3	(−0.029)	(0.037)		
			Treatment × Sex			$\chi^2_{(2)} = 6.5$	$p = \mathbf{0.039}$
			TreatG:SexF	−0.041	0.025		
			TreatP:SexF	0.015	0.022		
			Treatment				
			TreatG	0.018	0.015		
			TreatP	−0.055	0.016		
			Cohort			$\chi^2_{(2)} = 22.4$	$p < \mathbf{0.001}$
			Cohort2	−0.020	0.025		
			Cohort3	−0.010	0.024		
			SexF	0.010	0.021		
			Latency to emerge OF	(−0.00003)	(0.00002)	$\chi^2_{(1)} = 1.5$	$p = 0.22$
Touched NO	Binomial	141	Mean	1.035	0.261		
			Treatment × Cohort			$\chi^2_{(4)} = 6.62$	$p = 0.16$
			TreatG:Cohort2	(4.50e + 15)	(1.45e + 06)		
			TreatP:Cohort2	(0.397)	(0.481)		
			TreatG:Cohort3	(−0.986)	(1.13)		
			TreatP:Cohort3	(0.357)	(1.14)		
			Treatment × Sex			$\chi^2_{(2)} = 0.68$	$p = 0.71$
			TreatG:SexF	(1.590)	(0.644)		
			TreatP:SexF	(−0.346)	(0.834)		
			Treatment			$\chi^2_{(2)} = 1.28$	$p = 0.53$
			TreatG	(0.345)	(0.537)		
			TreatP	(0.246)	(0.341)		
			Cohort			$\chi^2_{(2)} = 0.52$	$p = 0.77$
			Cohort2	(−0.123)	(0.601)		
			Cohort3	(0.279)	(0.439)		
			SexF	(−0.217)	(0.364)	$\chi^2_{(1)} = 0.36$	$p = 0.55$
			Latency to emerge NO	(−0.001)	(0.001)	$\chi^2_{(1)} = 0.65$	$p = 0.42$
			Resting time OF	(0.287)	(1.213)	$\chi^2_{(1)} = 0.06$	$p = 0.81$

(Continued)

TABLE 3 | Continued

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Latency NO	Gaussian	115	Mean	8.940	0.962		
			Treatment × Cohort			$\chi^2_{(4)} = 10.0$	$p = \mathbf{0.04}$
			TreatG:Cohort2	−3.405	1.451		
			TreatP:Cohort2	−0.551	1.279		
			TreatG:Cohort3	−0.710	1.614		
			TreatP:Cohort3	−0.232	1.647		
			Treatment				
			TreatG	1.473	1.240		
			TreatP	−0.245	0.847		
			Cohort				
			Cohort2	2.054	1.125		
			Cohort3	0.374	1.345		
			Latency to emerge NO	0.005	0.001	$\chi^2_{(1)} = 0.65$	$p < \mathbf{0.001}$
			Resting time OF	(1.929)	(3.159)	$\chi^2_{(1)} = 0.373$	$p = 0.54$

*P-values derived from Wald tests comparing models with and without the explanatory variable (Zuur et al., 2009). P-values for significant terms (indicated in **bold**) derive from minimal adequate models. P-values for non-significant terms derive from models just before the terms were dropped. Coefficients for significant terms derive from minimal adequate models. Coefficients for non-significant terms (in brackets) derive from models just before the terms were dropped (please note that estimates of coefficients alter during the model simplification and that they are based on models with transformed response variables). Reference levels ("Mean") are always treatment = "d", i.e., deprivedly reared spiders; cohort = "1"; and sex = "male". "TreatG" refers to treatment "g", i.e., socially enriched reared spiders; "TreatP" refers to treatment "p", i.e., physically enriched reared spiders. "SexF" refers to female spiders. N = sample size, i.e., number of spiders tested.*

TABLE 4 | Model outputs (GEEs) testing for behavioral differences among treatments or cohorts in an open field test (first trial).

Response variable	N	Explanatory variables					
		Treatment: d;g	Treatment: d;p	Treatment: g;p	Cohort: 1;2	Cohort: 1;3	Cohort: 2;3
Latency to emerge OF	136	$\mathbf{p < 0.001}$ $[\chi^2_{(1)} = 11.5]$	$\mathbf{p = 0.037}$ $[\chi^2_{(1)} = 4.35]$	$p = 0.47$ $[\chi^2_{(1)} = 0.52]$	$p = 0.71$ $[\chi^2_{(1)} = 0.14]$	$\mathbf{p < 0.001}$ $[\chi^2_{(1)} = 20.1]$	$\mathbf{p < 0.001}$ $[\chi^2_{(1)} = 17.6]$
Percentage of area visited OF	135	$p = 0.85$ $[\chi^2_{(1)} = 0.04]$	$\mathbf{p = 0.002}$ $[\chi^2_{(1)} = 10.0]$	$\mathbf{p = 0.007}$ $[\chi^2_{(1)} = 7.3]$	–	–	–
Resting OF	136	–	–	–	$p = 0.4187$ $[\chi^2_{(1)} = 0.65]$	$\mathbf{p < 0.001}$ $[\chi^2_{(1)} = 15.55]$	$\mathbf{p < 0.001}$ $[\chi^2_{(1)} = 14.8]$

*The letters in the columns for explanatory variables indicate the treatments (d = deprived; g = group living; p = physically enriched) and the cohorts (1, 2, and 3) that were compared. P-values derived from Wald tests comparing models (Zuur et al., 2009) with and without the indicated levels merged together. N = sample size, i.e., number of spiders tested. Significance is indicated in **bold**.*

TABLE 5 | Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) over all individuals.

Response variable	Error structure	N Ind.	N Tr.	*R*	*SE*	CI	rptR method	Link function
Latency to emerge OF	Gaussian	158	300	0.33	0.077	**0.183–0.478**	LMM.REML	–
Percentage of area visited OF	Gaussian	159	310	0.264	0.08	**0.105–0.415**	LMM.REML	–
Visitation central area OF	Binomial	159	311	0.278	0.081	**0.07–0.391**	PQL method	logitlink
Activity in central area OF	Gaussian	146	249	0.341	0.089	**0.165–0.507**	LMM.REML	–
Resting OF	Gaussian	155	285	0.477	0.066	**0.332–0.597**	LMM.REML	–
Touched NO	Binomial	160	320	0.203	0.071	**0.085–0.357**	PQL method	logitlink
Latency NO	Gaussian	140	232	0.045	0.076	0–0.247	LMM.REML	–

*Estimates derive from models with bootstraps and permutations (each 1000). Variables are listed in the left column and repeatabilities (R), their standard errors (SE), and 95% confidence intervals (CI; given in original scale) are given. "rptR methods" refers to the used method in the analysis (see Nakagawa and Schielzeth, 2010). Not each individual participated in both test runs; therefore number of trials are not twice the number of individuals. N Ind., number of individuals; N Tr., number of trials. Significance (i.e., confidence interval not including zero) is indicated in **bold**.*

TABLE 6 | Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) tested separately for each treatment.

Variable	Error structure	Treatment d					Treatment g					Treatment p				
		N Ind.	N Tr.	*R*	*SE*	CI	N Ind.	N Tr.	*R*	*SE*	CI	N Ind.	N Tr.	*R*	*SE*	CI
Latency to emerge OF	Gaussian	51	96	0.208	0.135	0–0.481	50	94	0.306	0.136	**0.038–0.561**	57	110	0.310	0.120	**0.067–0.540**
Percentage of area visited OF	Gaussian	50	95	0.196	0.133	0–0.465	51	101	0.308	0.124	**0.044–0.520**	58	114	0.227	0.121	0–0.462
Visitation central area OF	Binomial	50	96	0.358	0.144	0–0.574	51	101	0.227	0.134	0–0.488	58	114	0.228	0.124	0–0.440
Activity in central area OF	Gaussian	44	69	0.217	0.167	0–0.572	48	82	0	0.101	0–0.339	54	98	0.678	0.081	**0.499–0.809**
Resting OF	Gaussian	48	87	0.450	0.450	**0.161–0.661**	50	96	0.613	0.093	**0.386–0.759**	57	102	0.355	0.123	**0.107–0.566**
Touched NO	Binomial	51	102	0.176	0.128	0–0.434	51	102	0.139	0.122	0–0.400	58	116	0.263	0.118	0–0.483
Latency NO	Gaussian	44	69	0.154	0.159	0–0.518	47	79	0	0.103	0–0.351	49	84	0.165	0.145	0–0.474

Estimates derive from models with bootstraps and permutations (each 1000). Variables are shown in the left column and repeatabilities (R), their standard errors (SE), and 95% confidence intervals (CI; given in original scale) are given. "rptR methods" refers to the used method in the analysis (see Nakagawa and Schielzeth, 2010). Not all individuals participated in both test series, so that the numbers of trials are not twice the number of individuals. N Ind., number of individuals. N Tr., number of trials. Significance (i.e., confidence interval not including zero) is indicated in ***bold****.*

GLMs, with our behavioral variables as responses and the interaction between maternal line and treatment as well as their main effects as explanatory variables. We included only families for which we had data from at least two individuals per treatment (total number of individuals per families and test ranged from 10 to 17 across treatments). Only data of the first round of behavioral tests were used in these analyses. In order to meet model assumptions, data were either transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011) or adequate error structures were used (see above; for details see **Table 7**). Significance of interactions was tested with likelihood ratio tests comparing the model with and without this interaction (see Crawley, 2002).

RESULTS

Early Environmental Effects on Inter-Individual Variation in Behavior (Mean Level Differences)

All behavioral variables were affected by the rearing condition with the exception of whether or not spiders touched the novel object ("touched NO"; **Table 3**). Spiders from the deprived treatment tended to be least exploratory: they needed longer to leave the start cap ("latency to emerge OF") than spiders from the physically and socially enriched treatments in the open field test (**Figure 2A**; **Table 4**). Spiders from the physically enriched treatment visited more percent of the total area ("percentage of area visited OF") than spiders from the other two treatments (**Figure 2B**; **Table 4**). There was a significant effect of treatment on resting duration ("resting OF") depending on the sex of the individual with males resting less in the deprived and physically enriched treatments but more in the social treatment than females (**Table 3**). Furthermore, there were treatment effects on the likelihood for entering the central area ("visitation central

TABLE 7 | Model outputs (GLMs) testing for family × environment interactions fitting an interaction between maternal line and treatment as explanatory variables on behavior shown in the open field test (OF) and the novel object test (NO).

Variable	Error structure	*DF*	Test-statistic	*P*-values
Latency to emerge OF	Gaussian	10,60	$F = 0.54$	0.858
Percentage of area visited OF	Gaussian	10,70	$F = 0.78$	0.648
Visitation central area OF	Binomial	1	$\chi^2 = 18.7$	**0.044**
Activity in central area OF	Gaussian	8,48	$F = 1.69$	0.125
Resting OF	Gaussian	10,66	$F = 1.72$	0.326
Touched NO	Binomial	1	$\chi^2 = 19.38$	**0.036**
Latency NO	Gaussian	10,52	$F = 2.14$	**0.038**

We included only families in which we had data from at least two individuals per treatment (five families for "activity in central area", six families for all other variables). P-values derived from likelihood ratio tests ("F" = F-test; "χ^2" = Chi-square test) of models with and without the interaction. Significance is indicated in ***bold****.*

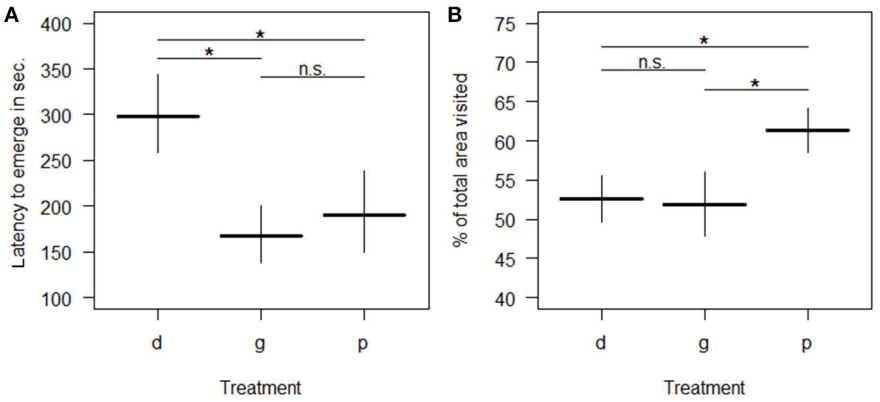

FIGURE 2 | Predicted mean levels (± SE) of behavioral responses in an open field test by spiders raised in one of three different treatment groups (d = "socially and physically deprived"; g = "socially enriched"; p = "physically enriched"). Panel **(A)** shows the latency to emerge; Panel **(B)** shows the percentage of area visited. All predictions derive from general estimated equations models (GEEs) after stepwise reduction to minimal adequate model including only significant terms. "n.s." indicates non-significant ($p > 0.05$) and "*" significant ($p \leq 0.05$) differences between the mean levels of groups.

area OF"), time spent active in the center ("activity in central area OF"), and in the latency to touch the novel object ("latency NO") but different for the cohorts (cohort x treatment, **Table 3**). Finally, cohort 3 needed less time to climb out the start cap in the open field tests and rested less than spiders from the other two cohorts (**Table 4**).

Repeatability

All behavioral measures were repeatable over time, except the latency to touch the novel object ("latency NO"; **Table 5**). The significant repeatabilities were moderate (0.203–0.447). However, when analyzed separately for each treatment, few behavioral variables remained significantly repeatable (**Table 6**): one in the deprived ("resting OF") and three out of seven in the socially ("resting OF"; "latency to emerge OF"; "percentage of area visited OF") and in the physically ("resting OF"; "latency to emerge OF"; "activity in central area OF") enriched treatment. Furthermore, confidence intervals of most repeatability values overlapped greatly among treatment groups.

Family by Environment Interactions

Family by environment interactions were found on those three behavioral variables that were not repeatable in any of the three treatment groups, namely: whether or not spiders entered the central area of the open field, whether they touched the novel object, and the latency to do so (**Table 7**). The effects were not driven by single families (as seen from visual inspection of interaction plots and model estimates, not shown); yet, the exact patterns of these interactions are beyond the scope of the manuscript.

DISCUSSION

The early environment in which spiders were raised significantly affected their exploratory tendencies (i.e., the population mean level of behavior). All but one behaviors measured were repeatable (at least over the whole study population), hence, we found evidence for personality differences. These findings combined indicate that external stimuli can influence the development of personality traits. We also found evidence for family by environmental interactions on behavioral traits. This means that families differed in their response to environmental conditions and suggests that families differed in their plasticity.

We found differences in the mean level of behaviors in our treatment groups, suggesting that the early environment influenced the development of exploratory behavior in the jumping spiders. In particular, individuals raised in the physically enriched treatment group were more exploratory than their siblings in the deprived treatment. This finding corroborates results from earlier studies on spiders (e.g., Carducci and Jakob, 2000; Buchsbaum and Morse, 2012; Bengston et al., 2014), nematodes (Rose et al., 2005), and vertebrates (e.g., Rosenzweig and Bennett, 1996; van Praag et al., 2000). Exploration, as an information-gathering process, might be more beneficial in an enriched (or generally more complex) than in a deprived (or generally very simple) environment with little to explore. Exploration can be costly (e.g., in terms of increased metabolism, or mortality risk) and thus individuals should not explore if not necessary. We found furthermore a sex-dependent treatment effect on the resting duration with group living males resting more than solitarily reared ones. Sexual size dimorphism is associated with a risk of cannibalism by the larger females (Wilder and Rypstra, 2008; Liedtke, J., personal observation), which may suggest that group living males are less active and thereby reduce encounter rates with females (compare sex-reversed pattern found in mice offspring: Heiming et al., 2009; and Hedrick and Kortet, 2012, for sex-dependent consistency over metamorphosis). Accordingly, a plastic response to the (early) environmental condition that an individual experiences seems sensible. Indeed, external influences particularly during development might have long lasting effects (reviewed in e.g., Snell-Rood, 2013).

The different responses of the three cohorts in our experiment may be an indication for sensitive phases (e.g., Groothuis

and Trillmich, 2011) or "developmental-windows" (Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011) within the developmental process of personality differences. The cohorts experienced different experimental conditions: in contrast to spiders from cohort 1 and 3, spiders from the cohort 2 were raised in groups for the first 2 months before they were assigned to the three treatments. Therefore, this cohort received an early social enrichment, regardless of later treatment. Results show that individuals from cohort 2 differed from the other two cohorts in several behaviors. Although it is difficult to explain the direction of these effects, these results indicate that, at least for the social enrichment, environmental conditions encountered in the first 2 months seem to have long lasting effects (permanent environmental effects *sensu* Dochtermann et al., 2015) on the development of behavioral tendencies. These patterns deserve further attention by follow-up studies in order to understand the proximate mechanisms of these apparently sensitive periods and if such effects can be induced by manipulation of the physical environment as well.

Group living also had positive effects on exploratory behavior in non-social contexts. This is in contrast to previous studies showing no effects of group living on behavior in non-social tests (reviewed in Taborsky et al., 2012). Yet, other studies found impairments of social isolation in multiple aspects of behavior (reviewed in e.g., Ballen et al., 2014). Hence, at least in some species contact to conspecifics can induce stable behavioral differences in other than the social realm. This suggests that early environment conditions can create behavioral differences in a context-general way.

Noteworthy, we found significant family by environment interactions on three of the investigated behavioral variables. This potentially indicates genetic variation for plasticity and suggests that plasticity itself might be under natural selection (Pigliucci, 2005; Dingemanse et al., 2010). Whether higher or lower plasticity is favored might depend on how stable and predictable environmental conditions are over time, with more stable conditions potentially favoring lower plasticity (see e.g., Dingemanse et al., 2010; Snell-Rood, 2013). But please note that we cannot rule out pre-hatching maternal effects in our study. Further studies are required to provide more insights, especially studies in which the paternity is also known.

Five behaviors that were repeatable over the whole population were not repeatable in all subpopulations (i.e., treatment groups) when estimated separately. Also, most confidence intervals of repeatabilities overlapped among treatment groups, suggesting repeatability was not necessarily significantly different among groups. Therefore, the extent of repeatability was likely not induced by the environmental conditions experienced. The pattern, that behaviors were repeatable across all individuals but not within all treatment groups, could potentially arise if between-individual variation in behavior within treatment groups is rather low (compared to between-individual variation across treatments) and/or if within-individual consistency in behavior is low. In both behavioral tests the average response of the deprived group was lower than that of the two enriched treatment groups, thereby leading to mean-level consistency (i.e., consistent differences between the average responses of each group; *sensu* Stamps and Groothuis, 2010). These consistent differences between treatment groups may explain why we found significant effects when we tested for repeatability over the whole population. The behavioral consistency of individual spiders within each treatment, on the other hand, may have been rather low, so that we found behavioral repeatability in fewer variables when treatments were assessed separately. This may indicate that for these variables, repeatability is mostly an effect of environmental induction by divergently shifting the mean level of each subpopulation (i.e., deprived group toward lower vs. enriched groups toward higher exploratory tendencies). Yet, these interpretations should be viewed with caution, since the absence of repeatable behavior within treatments in the five variables mentioned above could alternatively be an artifact of lower sample sizes within than among treatments. However, sample sizes in each subpopulation were still decent ($\geq$44; see **Table 6**) indicating that these patterns might be biologically relevant and deserve attention in further studies. For example, studies using samples derived from larger study areas may be more likely to find repeatability even with relative low individual stability because they might include individuals with different environmental backgrounds.

Nevertheless, we also should bear in mind that environmental induction does not necessarily lead to differential consistency but could even lead to the opposite. If individuals have different genotypes they may have different innate levels in behavioral expressions. However, plasticity, i.e., the ability to respond sensitively to the environment, could lead to an approximation of these initial differences according to local conditions. Furthermore, we expect that, with plasticity being costly (see e.g., Dall et al., 2004; Pigliucci, 2005), individuals having an innate behavioral level closer to the local optimum to have an improved fitness (all other things being equal) because they need less modification in their responses. This implies that mean level should be under selection which may explain the differences between families in this study.

Taken together, results found in this study indicate that exploratory tendencies of *M. muscosa* are influenced by the environmental conditions experienced; families may differ in plasticity and thus provide the raw material for natural selection to act upon; and finally, observed patterns of personality distribution found in the field may be crucially influenced by plastic responses of sensitive systems.

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